Reticulitermes (Isoptera: Rhinotermitidae) in Arizona: Multiple Cuticular Hydrocarbon Phenotypes Indicate Additional Taxa

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ABSTRACT Current taxonomic and biogeographical information on *Reticulitermes* in the United States suggests the only species found in Arizona is *Reticulitermes tibialis* Banks. *Reticulitermes* occurs naturally throughout Arizona with the exception of much of the Sonoran and Colorado deserts. Collections of *Reticulitermes* from disparate locations in Arizona and neighboring states were made to characterize their cuticular hydrocarbons for taxonomic purposes. We identified five phenotypes based on cuticular hydrocarbon mixtures of worker termites. The predominant hydrocarbons in AZ-A have 25 and 27 carbons in the parent chain, including 5,17-dimeC27. The late-eluting compounds are composed primarily of dienes, trienes, a homologous series of internally branched mono- and dimethylalkanes, and 5,17-dimethylalkanes. AZ-B differs from AZ-A by lacking the late-eluting dienes and trienes and by producing smaller amounts of hydrocarbons with 27 carbons in the parent chain. The cuticular hydrocarbons in AZ-C are composed primarily of olefins; C29:1 is the most abundant, and, with C27:1, C31:2, and C33:2, predominates the hydrocarbon mixture. This phenotype also has a homologous series of 5,17-dimethylalkanes from C27 to C43. AZ-D is distinguished by the absence of any 5-methylalkanes, 5,17-dimethylalkanes, or late-eluting dienes or trienes. The hydrocarbon mixture of AZ-D most closely resembles that of *Reticulitermes hesperus* Banks from northern California. NM-A can be distinguished from the other phenotypes by the significant amounts of the hydrocarbons coeluting in two peaks: C27 + C27:3 and 7-, 9-, 11-, 13-meC27 + C27:2. AZ-A was not common; the few samples we collected were all at the higher elevations, from 2,000 to 2,250 m, in northern Arizona. AZ-B was the most common and was found throughout the state from Fairbank (≈1,300m) to Jacob Lake (≈2,600 m). This phenotype also was found in eastern Nevada and southern Utah. AZ-C was sympatric with AZ-B over most of the distribution of the latter regions but was elevationally allopatric in southern Arizona. AZ-C occurred at high elevations (>1,500 m) on the desert islands of southeastern Arizona, such as the Santa Catalina, Santa Rita, Chiricahua, and Pinaleno mountains, whereas AZ-B occurred at lower elevations (<1,250 m), usually associated with a riparian area. AZ-D was collected only once in northern Arizona near Jacob Lake, AZ (≈1,800 m) but also on Mt. Charleston in southern Nevada. NM-A was collected near Jemez Springs and Chaco Canyon, NM, as well as in the vicinity of Moab, UT. Additional data from morphology, behavior and/or DNA may confirm that these phenotypes represent distinct species as it has with California *Reticulitermes*.

KEY WORDS biogeography, chemotaxonomy, *Reticulitermes tumiceps*, speciation, subterranean termite

Current information on *Reticulitermes* in the United States suggests the only species found in Arizona is *Reticulitermes tibialis* Banks (Snyder 1954; Weesner 1965, 1970; Nutting 1990). Much of the taxonomic and biogeographical information on *Reticulitermes* spp. was developed early in the last century (Banks and Snyder 1920; Light 1934; Pickens 1934a,b; Banks 1946; Miller 1949; Snyder 1954), and there is agreement that the genus needs revision (Weesner 1970, Nutting 1990, Scheffrahn and Su 1994, Thorne 1999). Studies of *Reticulitermes* spp., a Holarctic genus of ecologically and economically important subterranean termites, are constrained by the antiquated state of the taxonomy of this genus.

Termite taxonomy is a complex issue (Clément et al. 2001). Termites often lack features that facilitate specific diagnoses, are extremely plastic, and exhibit considerable morphological variation. Light (1927) argued that termites are notoriously "lacking in ornamentation and furnish few if any of those satisfying definite differences . . . which facilitate specific diag-

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noses . . . . Further, termite species are extremely plastic and exhibit a wide range of (morphological) variation. Finally, the specific characters which are available express themselves almost entirely in the form of differences in range of size . . . . " This lack of good diagnostic, morphological characters likely led to the simplification of the taxonomic keys and lumping all *Reticulitermes* in Arizona into one species, *R. tibialis* Banks, by Snyder (1949).

No objective, discrete character state or continuous measurement is presented to unequivocally identify a given specimen to species. Vague and subjective color differences may be more apparent to some observers than others. Furthermore, geographical distribution may not be meaningful as part of the description of a species so easily transported by human activity. It is hoped that more reliable and definable characters can be found by using a variety of methods to differentiate the insects and to determine whether they can be named as distinct species. That has been our goal in using chemical and behavioral characters to study *Reticulitermes* (Haverty et al. 1996, 1999a,b,c, 2000, 2003; Haverty and Nelson 1997, Getty et al. 2000a,b; Delphia et al. 2003). Such characteristics also might be more biologically meaningful.

To circumvent the difficulty with keys for *Reticulitermes,* we have used characterization of cuticular hydrocarbons to help delineate taxa. There is a growing body of evidence suggesting that termites have species-specific mixtures of cuticular hydrocarbons (Page et al. 2002, and references therein). Repeatable chemical phenotype groups and supporting biological information are needed to confirm that cuticular hydrocarbon phenotypes represent distinct taxa (Haverty et al. 1999a,b, 2003; Clément et al. 2001, Nelson et al. 2001). Until taxonomic descriptions are published and new species named, we must rely on the assignment of cuticular hydrocarbon phenotype labels to *Reticulitermes* spp. in Arizona (Haverty et al. 1999c).

We report here the results of characterization of the cuticular hydrocarbons of *Reticulitermes* collected from 1990 to 2003 in Arizona as well as in adjoining states of Nevada, New Mexico, and Utah. Our results provide further support for the hypothesis that the cuticular hydrocarbon phenotypes of *Reticulitermes* represent distinct taxa or species.

Materials and Methods

Nutting Termite Collection. The Nutting Collection in the Entomology Museum of the University of Arizona was established and curated by William L. Nutting until the time of his death in 1992. The specimens in this collection date back to 1932 and contain samples of *Reticulitermes* from every county in Arizona, except La Paz. The specimens of *Reticulitermes* from Arizona were all identified by Dr. Nutting as *Reticulitermes tibialis* Banks based on keys by Snyder (1954) and Weesner (1970). Shortly after Dr. Nutting's death, the authors examined the Nutting Collection and recorded all of the information on each of the specimen labels. All specimens were retained in the Nutting Collection; none were permanently removed. The collection localities were used to generate data on the elevation and coordinates for each sample using the Back Roads Explorer TOPO! software (National Geographic). Duplicate records (i.e., numerous collections from Tucson) were reduced to a single record.

Collection of Termites. From spring 1990 until fall 2003, we collected *Reticulitermes* spp. throughout much of the known distribution in Arizona reported by Haverty and Nutting (1976) and complementary collections from adjacent states of Nevada, Utah, and New Mexico. These serendipitous and directed collections increased the sample size, but more importantly, they have provided analysis of the cuticular hydrocarbons of 68 collections. When feasible, we usually collected more than one colony at each stop. These localities are listed in Tables 1 and 2.

Naturally infested wood samples were bagged and kept cool until the termites could be separated from wood and other debris. Samples of 50–200 workers were placed in separate labeled 20-ml scintillation vials (Wheaton Scientific, Millville, NJ) and then frozen and dried in preparation for cuticular hydrocarbon extraction (Haverty et al. 1999c). Concurrently, fresh (i.e., not dried) voucher samples (workers and soldiers) were preserved in 80% ethanol and retained by the authors for future morphological and genetic studies. Representative vouchers of each hydrocarbon phenotype were deposited in the Nutting Collection in the Department of Entomology of the University of Arizona.

Extraction Procedure and Characterization of Hydrocarbons. The hydrocarbons from the termites were extracted, characterized, and quantified in the same manner as reported in Haverty and Nelson (1997). Fifty to 200 worker termites were immersed in 10 ml of hexane (HX0296-1, EM Scientific, Gibbstown, NJ) for 10 min to extract the cuticular lipids. Hydrocarbons were separated from other compounds by pipetting the extract through 4 cm of activated silica gel (70–230 mesh, Sigma-Aldrich, St. Louis, MO) in 22-cm Pasteur pipet (Fisher, Pittsburgh, PA) mini-columns. An additional 5 ml of clean hexane was dripped through the silica gel. The resulting hydrocarbon extracts were evaporated to dryness under a stream of nitrogen and redissolved in 60 μl of hexane for gas chromatography-mass spectrometry (GC-MS) analyses. A 3-μl aliquot was injected into the GS-MS.

GC-MS analyses were performed on a Hewlett–Packard (HP) 5890 gas chromatograph equipped with a HP 5970B mass selective detector interfaced with HP Chemstation data analysis software (HP59974J rev. 3.1.2). The GC-MS was equipped with an HP-1 fused silica capillary column (25 m by 0.2 mm i.d.) and operated in split mode (with a split ratio of 8:1). Each mixture was analyzed by a temperature program from 200 to 320°C at 3°C/min with a final hold of 11 or 16 min. Electron impact mass spectra were obtained at 70 eV. The five samples collected in 2003 were analyzed under the same conditions using an Agilent 6890 GC

Table 1. Collection localities of *Reticulitermes* samples from Arizona used to determine cuticular hydrocarbon phenotypes

AZ Phenotype	County	Collection locality	Date	Elevation (m)	Latitude (°N)	Longitude (°W)	Sample no.
A	Coconino	Hwy 40 @ Meteor Crater Road	07/26/99	1,641	35.10885	111.0315	AZ99_5
A	Navajo	Hwy 99, 24.1 km past McHood County Park	07/26/99	1,646	34.82971	110.67518	AZ99_6
A	Navajo	Junction AZ 277 and AZ 377	07/27/99	1,938	34.46383	110.47704	AZ99_28
A	Navajo	Second Mesa, Hopi Indian Reservation	06/19/95	1,738	35.79313	110.50778	RETICAZ1
B	Apache	Hwy 60, 9.7 km W of New Mexico state line	07/29/99	2,162	34.15589	109.12872	AZ99_48
B	Apache	Junction AZ 260 and AZ 261	07/28/99	2,180	34.10544	109.34441	
B	Coconino	4.0 km E of Jacob Lake	07/11/00	2,322	36.73307	112.17545	
B	Coconino	8.0 km S of LeFevre Overlook, Hwy 89A, Kaibab NF	07/11/00	1,480	34.93713	111.74729	
B	Coconino	10.5 km E of Jacob Lake	07/11/00	2,085	36.74772	112.11866	
B	Coconino	12.9 km E of Jacob Lake	07/11/00	1,956	36.72894	112.0868	RTZ00108
B	Coconino	Hwy 99 @ Apache/Sitgraves NF boundary	07/26/99	1,938	34.63746	110.83113	
B	Coconino	LeFevre Overlook, Hwy 89A, Kaibab NF	07/11/00	1,957	35.03023	111.73406	
B	Coconino	North Rim of Grand Canyon	06/21/95	2,533	36.2114	112.06038	RETGC1
B	Coconino	Twin Arrows	07/26/99	1,792	35.16105	111.27233	
B	Mohave	Hwy 389 W of Fredonia nr Kaibab-Paiute Indian Res.	07/11/00	1,423	36.93551	112.55581	RTZ00110
B	Navajo	Heber	07/27/99	1,990	34.43258	110.5962	AZ99_31
B	Navajo	Second Mesa, Hopi Indian Reservation	06/19/95	1,738	35.79313	110.50778	RETICAZ4
B	Pima	Hutch's Pools, Sabino Canyon, Coronado NF	04/04/00	1,249	32.3792	110.79339	AZ00_3
B	Pima	Tucson @ Rillito River	04/02/00	728	32.2702	110.91647	AZ00_2
B	Yavapai	24.1 km E of Camp Verde on Hwy 260	09/11/98	1,513	34.50442	111.67135	RTAZ9857
B	Yavapai	4.8 km S of Drake Overpass, Prescott NF	09/09/98	1,462	34.95018	112.42171	
B	Yavapai	4.8 km W of summit of SR 89A	09/10/98	1,958	34.69618	112.16572	
B	Yavapai	6.9 km W of Jerome on SR 89A	09/10/98	1,846	34.73912	112.14428	
B	Yavapai	11.4 km W of Jerome on SR 89A	09/10/98	1,883	34.68711	112.16958	
B	Yavapai	Cherry on Hwy 169	09/10/98	1,546	34.58989	112.05166	
B	Yavapai	Indian Creek Campground, Prescott NF	09/08/98	1,773	34.47954	112.49647	
B	Yavapai	Lower Wolf Creek Campground, Prescott NF	09/08/98	1,873	34.45544	112.45351	
B	Yavapai	Mingus Mountain Road, Prescott NF	09/10/98	2,295	34.70128	112.13966	RTAZ9855
B	Yavapai	Prescott NF @ Hwy 89 near Prescott	09/08/98	1,697	34.51174	112.47753	RTAZ9842
B	Yavapai	Prescott Pines, Prescott NF	09/08/98	1,715	34.57333	112.50369	
C	Apache	County Road 4225, 3.2 km W of New Mexico state line	07/29/99	2,301	34.05292	109.08551	AZ99_50
C	Cochise	Morse Canyon Trailhead, Chiracahua Mts.	07/22/98	2,022	31.85012	109.32524	
C	Cochise	Onion Saddle, Chiracahua Mts.	07/22/98	2,314	31.93503	109.26408	RTAZ9811
C	Cochise	Rustler Park Road, Chiracahua Mts.	07/22/98	2,327	31.9301	109.26184	
C	Cochise	West Turkey Creek Campground, Chiracahua Mts.	07/22/98	1,850	31.86405	109.35817	RTAZ981
C	Coconino	Chevelon Work Center, Apache/Sitgraves NF	07/26/99	1,889	34.59115	110.78918	
C	Coconino	Devil Dog Road @ Interstate 40, 16.1 km W of Williams	09/09/98	1,619	35.21388	112.4247	RTAZ9850
C	Coconino	Hwy 99 @ Apache/Sitgraves NF boundary	07/26/99	1,938	34.63746	110.83113	
C	Coconino	Oak Creek Canyon, 3.2 km N of Scenic Lookout, Hwy 89A	09/11/98	1,995	35.06699	111.7329	
C	Coconino	Twin Arrows	07/26/99	1,792	35.16105	111.27233	AZ99_4
C	Graham	Arcadia Campground, Pinaleno Mts.	07/23/98	2,031	32.64919	109.81812	RTAZ9816
C	Graham	Near Turkey Flat, Pinaleno Mts.	07/23/98	2,232	32.63404	109.81829	
C	Graham	Noon Creek Picnic Area, Pinaleno Mts.	07/23/98	1,595	32.66752	109.79811	RTAZ9814
C	Navajo	Aripine	07/27/99	1,984	34.40758	110.43162	
C	Navajo	Burton Road @ Hwy 260, Linden	07/27/99	1,921	34.28465	110.15899	
C	Navajo	Heber	07/27/99	1,990	34.43258	110.5962	AZ99_35
C	Navajo	Junction AZ 277 and AZ 377	07/27/99	1,938	34.46383	110.47704	
C	Navajo	Pinedale	07/27/99	1,978	34.30861	110.24945	
C	Pima	Eagle Mtn. Mine (East Ridge Mine), Santa Catalina Mts.	07/25/98	1,766	32.47357	110.72923	
C	Pima	Palisades Ranger Station, Santa Catalina Mts.	10/01/90	2,383	32.42949	110.74388	
C	Pima	Santa Catalina Mts.	06/07/95	2,407	32.43522	110.75176	RETTUMAZ
C	Pima	Stratton's Camp, N side of Santa Catalina Mts.	10/18/99	1,978	32.46885	110.74584	
C	Santa Cruz	Mt. Hopkins	11/01/91	2,344	31.68485	110.87842	
C	Yavapai	29.0 km E of Camp Verde on Hwy 260	09/11/98	1,703	34.5119	111.64904	
C	Yavapai	35.4 km E of Camp Verde on Hwy 260	09/11/98	1,850	34.49789	111.62306	RTAZ9858
C	Yavapai	6.9 km W of Jerome on SR 89A	09/10/98	1,846	34.73912	112.14428	
C	Yavapai	Indian Creek Campground, Prescott NF	09/08/98	1,773	34.47954	112.49647	
C	Yavapai	Mingus Mountain Road, Prescott NF	09/10/98	2,295	34.70128	112.13966	RTAZ9835
C	Yavapai	Prescott	10/01/90	1,641	34.54177	112.46686	
C	Yavapai	Prescott	09/08/98	1,641	34.54177	112.46686	
C	Yavapai	Prescott NF @ Hwy 89 near Prescott	09/08/98	1,670	34.52081	112.47983	
C	Yavapai	Prescott Pines, Prescott NF	09/08/98	1,715	34.57333	112.50369	
C	Yavapai	Senator Hwy, near Prescott	09/08/98	1,759	34.5259	112.46156	RTAZ9832
D	Coconino	16.1 km E of Jacob Lake	06/22/95	1,773	36.72703	112.0589	RETICAZ3

(Agilent Technologies, Palo Alto, CA) coupled with the 5973 MSD, Agilent Chemstation data analysis software G1701CA version C.00.00.

n-Alkanes were identified by their mass spectra. Mass spectra of methyl-branched alkanes were interpreted as described by Blomquist et al. (1987) to

Table 2. Collection localities of *Reticulitermes* samples from Nevada, Utah, and New Mexico used to determine cuticular hydrocarbon phenotypes

State	AZ phenotype	County	Collection locality	Date	Elevation (m)	Latitude (°N)	Longitude (°W)	Sample no.
Nevada	B	Lincoln	Pahranagat Wildlife Preserve, Hwy 93	07/12/00	1,012	37.26764	115.12271	NV-003
	D	Clark	Mt. Charleston, Hwy 157 @ 158	07/12/00	2,111	36.26344	115.61094	NV-005
	D	Clark	Mt. Charleston, Hwy 156 @ Marks Canyon Rd	0/12/00	2,320	36.35081	115.64396	NV-008
Utah	B	Washington	Hwy 18 near Central, Dixie NF	07/10/00	1,570	37.40387	113.63847	UT-001
	B	Washington	Hwy 9, 59.5 km W of Zion NP	07/10/00	964	37.17452	113.35112	UT-002
	NM-A	Grand	Negro Bill Canyon, near Moab	10/01/03	1,228	38.60366	109.52818	UT-038
	NM-A	Grand	Hwy 313 near Big Mesa Camping Area	09/30/03	1,869	38.54637	109.76794	UT-034
	C	Grand	Hwy 313 near Big Mesa Camping Area	09/30/03	1,869	38.54637	109.76794	UT-033
New Mexico	NM-A	Sandoval	Jemez Springs	09/13/03	1,873	35.76659	106.69609	NM-034
	A	San Juan	Chaco Cultural National Historic Park	09/14/03	1,960	36.06399	107.89735	NM-035

identify methyl branch locations. Mass spectra of di- and trimethylalkanes were interpreted as described by Page et al. (1990a,b) and Pomonis et al. (1978). Alkenes were identified by their mass spectra, but double bond positions were not determined (Haverty and Nelson 1997). Equivalent chain lengths (ECL) were calculated for some of the unsaturated compounds to distinguish the various isomers.

In the text and tables, we use shorthand nomenclature to identify individual hydrocarbons or mixtures of hydrocarbons. This shorthand uses a descriptor for the location of methyl groups (X-me), the total number of carbons (CXX) in the hydrocarbon component excluding the methyl branch(es), and the number of double bonds after a colon (CXX:Y). Thus, pentacosane becomes *n*-C25; 3-methylpentacosane becomes 3-meC25; 9,13-dimethylpentacosane becomes 9,13-dimeC25; and heptacosadiene becomes C27:2. Hydrocarbons are presented in the tables in the order of elution on our GC-MS system.

Integration of the total ion chromatogram was performed using the HP or Agilent Chemstation data analysis software. GC-MS peak areas were converted to percentages of the total hydrocarbon fraction. A summary of the relative amounts (mean, standard deviation, minimum, maximum, and proportion of samples with ≤0.1%) of each peak is presented in table form by using representative chromatograms of each phenotype.

Cluster Analysis of Hydrocarbon Mixtures from Termites. The percentage of each hydrocarbon peak was used as the response variable; the presence of coeluting compounds precluded exact quantification of many individual hydrocarbons. The Euclidean distance for 37 samples was calculated using all hydrocarbon peaks (Takematsu and Yamaoka 1999, Haverty et al. 2005) (R Development Core Team 2004). Results are displayed as a dendrogram. Hydrocarbons responsible for specific clusters were identified in the cluster analysis.

Results and Discussion

Nutting Collection. The Nutting Collection is extensive and contains >200 samples of *Reticulitermes.* About half of these samples were used to describe the distribution of *R. tibialis* relative to *Heterotermes aureus* (Snyder), an ecological equivalent occurring in the Sonoran Desert (Haverty and Nutting 1976). The collection localities, with elevations and coordinates, are presented in the *Appendix* and displayed graphically (Fig. 1). Considering the information that follows, many, if not all, of these specimens in the Nutting Collection will represent species of *Reticulitermes* other than *R. tibialis;* one was previously named (*Reticulitermes tumiceps* Banks) and others are yet to be fully described and named.

Reticulitermes spp. occur naturally throughout Arizona with the exception of much of the Sonoran and Colorado deserts. In general, *Reticulitermes* spp. were collected at elevations >1,200 m (Haverty and Nutting 1976; *Appendix;* Fig. 2). Exceptions to this generality are urban centers, such as Tucson and Yuma, or riparian areas, such as the Fort McDowell Indian Reservation, Tucson, and Yuma. *Reticulitermes* spp. could be considered exotic in the urban locations and may even include species exotic to Arizona. *Reticulitermes* spp. are the predominant subterranean termites above 1,200 m, occasionally occurring with *Gnathamitermes perplexus* (Banks) and *Amitermes wheeleri* (Desneux).

Cuticular Hydrocarbons of *Reticulitermes* from Arizona and Adjoining States. We made additional collections of *Reticulitermes* spp. from Arizona and

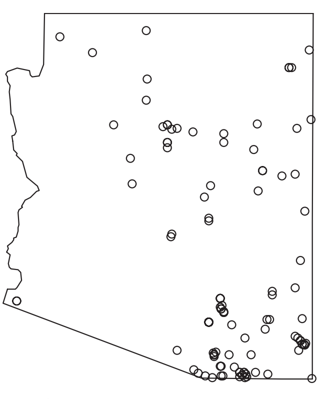

Fig. 1. Distribution of *Reticulitermes* specimens from Arizona in the Nutting Collection in the Entomology Museum of the University of Arizona.

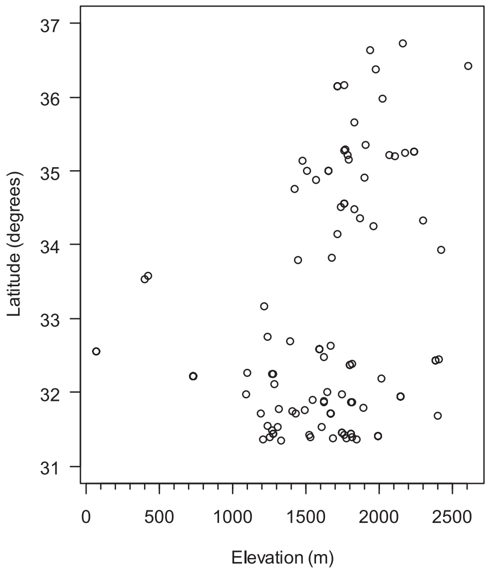

Fig. 2. Elevation and latitude of the *Reticulitermes* specimens from Arizona in the Nutting Collection in the Entomology Museum of the University of Arizona.

neighboring states to characterize their cuticular hydrocarbons for taxonomic purposes (Tables 1 and 2). From these samples, we have characterized 128 individual or isomeric mixtures of hydrocarbons. For *Reticulitermes* these hydrocarbons seem to be more informative than morphological characters of soldiers. Because alates are seldom collected with foraging groups, they have not been helpful for identifying our collections to species. Cuticular hydrocarbon mixtures of *Reticulitermes* samples from disparate locations in Arizona provided unexpected results. Rather than only one taxon being found, we identified four taxa in Arizona and one additional taxon from New Mexico and Utah based on their cuticular hydrocarbon mixtures. These collections cover most of the territory reported to be inhabited by *R. tibialis* in Arizona (Haverty and Nutting 1976) and adjoining states that should only have *R. tibialis* (Weesner 1970, Nutting 1990). We labeled them AZ-A, AZ-B, AZ-C, AZ-D, and NM-A based on locality (state) and the order in which they were discovered. These labels, at this time, are not intended to be nomenclatural acts. Future reports should follow assigning these phenotypes to described species.

The predominant hydrocarbons in AZ-A have 25 and 27 carbons in the parent chain, including 5,17-dimeC27. The late-eluting compounds are composed primarily of dienes, trienes, a homologous series of internally branched mono- and dimethylalkanes, and 5,17-dimethylalkanes (Fig. 3; Table 3). AZ-B differs from AZ-A by lacking the late-eluting dienes and trienes and producing smaller amounts of hydrocarbons with 27 carbons in the parent chain (Fig. 3; Table 4). AZ-C is very different from all of the other western *Reticulitermes* spp. The cuticular hydrocarbons in AZ-C are composed primarily of olefins; C29:1 is the most abundant, and, with C27:1, C31:2, and C33:2, predominates the hydrocarbon mixture. This phenotype also has a homologous series of 5,17-dimethylalkanes from C27 to C43 (Fig. 3; Table 5). AZ-D is distinguished by the absence of any 5-methylalkanes, 5,17-dimethylalkanes, or late-eluting dienes or trienes (Fig. 3; Table 6). NM-A can be distinguished from the other phenotypes by the significant amounts of the hydrocarbons coeluting in two peaks: C27 + C27:3 and 7-, 9-, 11-, 13-meC27 + C27:2 (Fig. 3; Table 7). The hydrocarbon mixture of AZ-D most closely resembles that of *Reticulitermes hesperus* Banks from northern California and samples from Mt. Charleston, NV (Fig. 3; Tables 2 and 6) (Haverty et al. 2003, Copren et al. 2005).

Soldier defense secretion mixtures have been characterized for samples of AZ-A, AZ-B, AZ-C, AZ-D (samples NV-005 and NV-008 in Table 2), and NM-A (Nelson et al. 2001). Soldiers of AZ-A have mostly geranyl linalool (82.4%) and γ-cadinene (16.8%) in their defense secretions. AZ-B has a similar terpene profile, although quantities were variable. AZ-B generally has more γ-cadinenal (0.5–13.2%) than AZ-A (0–1.3%), and the percentage of geranyl linalool ranged from 26.4 to 78.3 (mean = 64.4%) and the percentage of γ-cadinene from 9.7 to 66.7 (mean 23.1%). Soldier defense secretions from AZ-C show evidence of geographic differences. Samples from the Mogollon (Interior) biogeographic province, from Prescott to Springerville, had soldier defense secretions consisting mainly of myrcene (1.3–20.3%), *Z*- and *E*-ocimenes (0–19.8%), β-bisabolene (17.8–57.3%), γ-cadinene (1.8–40.5%), and geranyl linalool (0–50.4%). We summarized these samples as one group, AZ-C(I), although they were variable (Nelson et al. 2001). There was much less variability in soldier defense secretion profiles from samples collected in the higher elevations of the Santa Catalina, Santa Rita, Chiricahua, and Pinaleno mountains of the Sonoran biogeographic province. Samples of this soldier defense secretion phenotype, AZ-C(II), all produced ≥94.7% geranyl linalool (Nelson et al. 2001). Cuticular hydrocarbon phenotype AZ-D had a soldier defense secretion profile similar to AZ-A and AZ-B with >75% geranyl linalool and between 9 and 22% γ-cadinene (unpublished observations). Soldier defense secretions of NM-A consist almost entirely of geranyl linalool (mean 99.8%).

Insects synthesize most, if not all, of their complement of cuticular hydrocarbons de novo (Blomquist and Dillwith 1985). Howard (1993) reported that cuticular hydrocarbon composition varies among species within a genus, but little within a species. Cuticular hydrocarbon mixtures can be used to discriminate insect taxa. Haverty et al. (1991) proposed that if hydrocarbons are to be reliable as taxonomic characters, they should be abundant components (at least 1%, but preferably 5% of the total hydrocarbon mixture). They also should be unique or present in only a few of the species, or conversely, they should be common in most of the species yet completely absent or of insignificant quantities in one or a few. We have

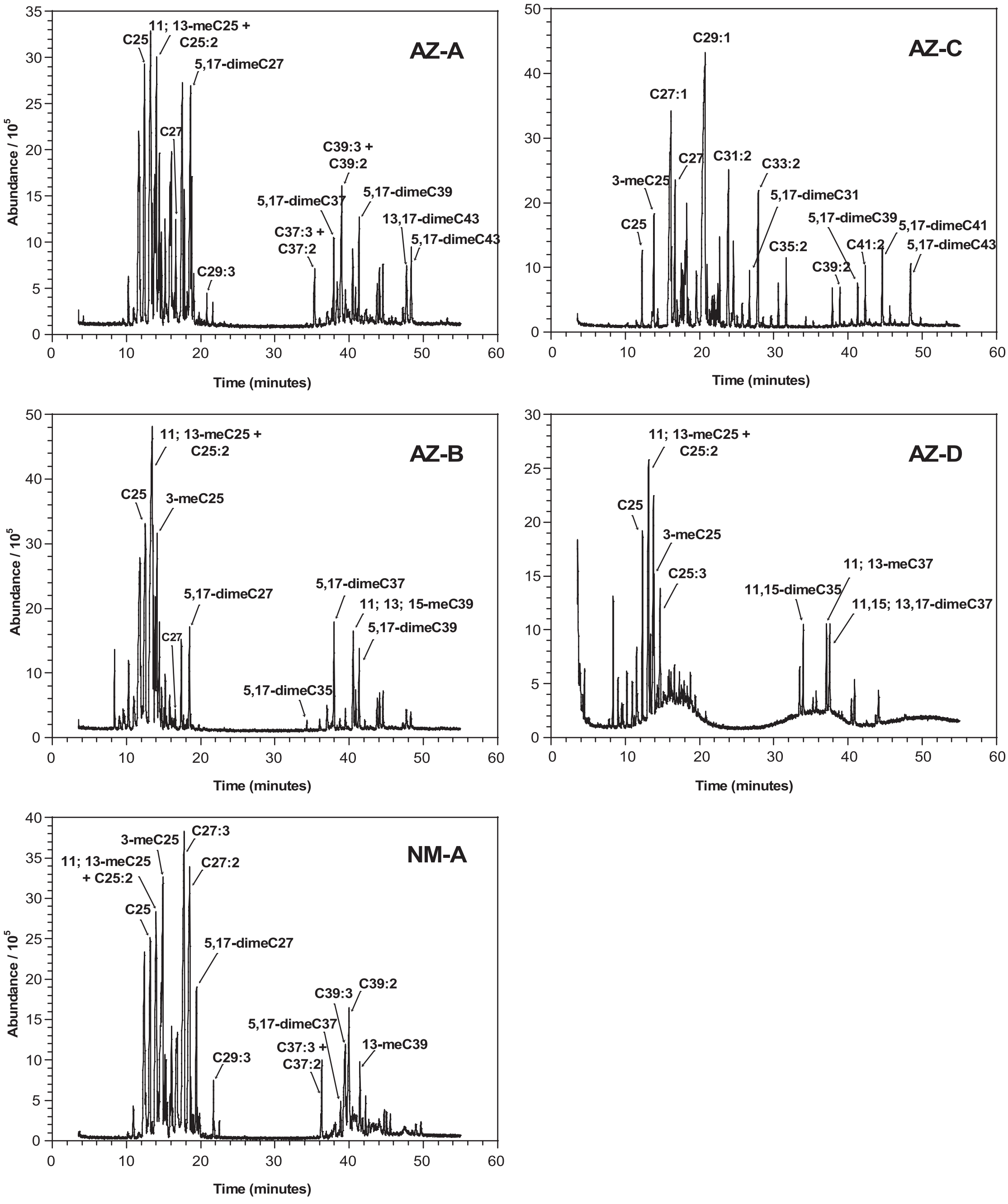

Fig. 3. Total ion chromatograms of cuticular hydrocarbons from workers of *Reticulitermes* spp. Phenotype AZ-A from Second Mesa, Hopi Indian Reservation; phenotype AZ-B from Second Mesa, Hopi Indian Reservation; phenotype AZ-C from the vicinity of Stratton's Camp, Santa Catalina Mountains; phenotype AZ-D from 16 km east of Jacob Lake; and phenotype NM-A from Jemez Springs, NM.

selected diagnostic cuticular hydrocarbons (Table 8) that meet these criteria and can be used to diagnose taxa.

Most termites have, with a few exceptions, species-specific mixtures of cuticular hydrocarbons (Kaib et al. 1991, Haverty et al. 1999c). Cuticular hydrocarbons are valuable characters for the analysis of cryptic insect species with few discernible morphological characters and have aided in the examination of cryptic species in a number of arthropod species, including ticks, bark beetles, mosquitoes, and grasshoppers (Copren et al. 2005). The evidence suggesting species-

Table 3. Percentage of total hydrocarbon from workers of *Reticulitermes* phenotype AZ-A

Hydrocarbon[a]	Mean (n = 5)	SD (%)	Min.	Max.	Prop. <0.1%
2-meC23	0.09	0.09	0.00	0.18	0.40
C24	0.99	0.22	0.76	1.33	0.00
12-, 11-, 10-, 9-meC24	0.52	0.17	0.35	0.79	0.00
2-meC24, C25:2, C25:1, 3-meC24	7.62	1.69	5.64	10.33	0.00
C25	7.29	0.26	7.03	7.66	0.00
13-, 11-, 9-, 7-meC25	15.36	1.76	12.47	16.95	0.00
5-meC25	1.84	0.34	1.37	2.25	0.00
2-meC25	4.72	0.93	4.00	6.25	0.00
3-meC25	6.89	0.61	6.39	7.93	0.00
5,15-; 5,17-dimeC25	1.00	0.40	0.60	1.54	0.00
C25:3 (ECL = 25.98)	2.11	1.09	0.75	3.20	0.00
C26	0.76	0.45	0.00	1.16	0.20
C25:3 (ECL = 26.07)	1.47	0.35	1.13	1.92	0.00
C27:1 (ECL = 26.30)	0.18	0.11	0.00	0.30	0.20
13-, 12-, 11-meC26; C26:2	1.98	0.17	1.76	2.13	0.00
C25:3 (ECL = 26.45)	0.61	0.46	0.00	1.14	0.20
6-meC26	0.09	0.20	0.00	0.44	0.80
2-meC26, C27:2, C27:1	3.84	1.00	2.92	5.56	0.00
C27:1 (ECL = 26.85)	2.25	0.47	1.67	2.82	0.00
6,18-dimeC26	0.34	0.39	0.00	0.94	0.40
5,17-dimeC26	0.15	0.15	0.00	0.30	0.40
4,16-; 4,18-dimeC26; C26:3	0.19	0.18	0.00	0.36	0.40
C27, C27:3	1.79	1.02	0.87	3.54	0.00
13-, 11-, 9-, 7-meC27; C27:2	7.79	1.11	6.08	9.17	0.00
5-meC27	2.16	0.35	1.76	2.61	0.00
2-meC27	0.16	0.15	0.00	0.28	0.40
3-meC27	0.63	0.15	0.41	0.77	0.00
5,17-dimeC27	7.32	2.46	3.45	9.47	0.00
C27:3 (ECL = 27.85)	1.64	0.61	0.60	2.19	0.00
C28	0.13	0.18	0.00	0.37	0.60
C27:3 (ECL = 28.09)	0.87	0.43	0.40	1.34	0.00
C27:3 (ECL = 28.25)	0.30	0.21	0.00	0.53	0.2
C29:3 (ECL = 29.00)	0.27	0.43	0.00	1.00	0.6
C29	0.16	0.25	0.00	0.57	0.6
15-, 13-, 11-, 9-, 7-meC29	0.05	0.10	0.00	0.23	0.8
C37:3	0.35	0.23	0.00	0.56	0.2
C37:2	0.87	0.46	0.50	1.61	0
6,18-; 5,17-dimeC36	0.07	0.10	0.00	0.19	0.6
17-, 15-, 13-, 11-meC37	0.42	0.12	0.26	0.60	0
7,17-dimeC37	0.17	0.16	0.00	0.35	0.4
5,17-dimeC37	1.40	0.57	0.49	2.01	0
C39:5, C39:4	1.53	0.27	1.24	1.92	0
C39:3, C39:2	3.77	0.45	3.04	4.27	0
6,18-; 5,17-dimeC38	0.45	0.31	0.00	0.73	0.2
15-, 13-, 11-meC39	1.49	0.41	0.79	1.90	0
13,17-dimeC39	0.79	0.08	0.67	0.84	0
7,17-dimeC39	0.07	0.10	0.00	0.20	0.6
5,17-dimeC39	1.75	0.77	0.63	2.66	0
15-, 13-, 11-meC41	0.52	0.21	0.29	0.74	0
13,17-dimeC41	0.86	0.34	0.52	1.31	0
5,17-dimeC41	0.54	0.36	0.18	0.95	0
12-, 11-meC42	0.02	0.05	0.00	0.11	0.8
12,16-; 11,15-dimeC42	0.03	0.06	0.00	0.14	0.8
5,17-dimeC42	0.02	0.04	0.00	0.09	1
15-, 13-, 11-meC43	0.14	0.21	0.00	0.45	0.6
13,17-dimeC43	0.58	0.65	0.00	1.54	0.4
5,17-dimeC43	0.62	0.62	0.00	1.65	0.2

[a] Hydrocarbons that coelute are listed together in the table.

Table 4. Percentage of total hydrocarbon from workers of *Reticulitermes* phenotype AZ-B

Hydrocarbon[a]	Mean (n = 13)	SD (%)	Min.	Max.	Prop. <0.1%
C23:1	0.03	0.11	0.00	0.40	0.92
C23	1.96	1.01	0.39	3.37	0.00
11-, 9-, 7-meC23	0.77	0.45	0.00	1.56	0.08
2-meC23	0.54	0.28	0.22	1.27	0.00
3-meC23	0.61	0.28	0.00	1.27	0.08
C24	1.44	0.32	0.84	1.93	0.00
12-, 11-, 10-, 9-meC24	1.49	0.47	0.77	2.54	0.00
2-meC24, C25:2, C25:1, 3-meC24	12.73	1.18	10.42	14.77	0.00
C25	9.09	1.83	6.45	12.42	0.00
13-, 11-, 9-, 7-meC25	28.40	5.12	20.49	36.60	0.00
5-meC25	2.41	0.91	1.18	4.31	0.00
2-meC25	4.07	1.01	2.58	6.26	0.00
3-meC25	6.15	0.91	5.04	7.52	0.00
5,15-; 5,17-dimeC25	1.92	0.88	0.80	4.21	0.00
C25:3 (ECL = 25.98)	1.51	1.38	0.00	4.21	0.31
C26	0.04	0.10	0.00	0.31	0.85
3,7-dimeC25	0.10	0.17	0.00	0.48	0.69
C25:3 (ECL = 26.07)	2.05	1.97	0.00	5.36	0.31
C27:1 (ECL = 26.30)	0.27	0.12	0.00	0.45	0.08
13-, 12-, 11-meC26; C26:2	1.09	0.25	0.69	1.50	0.00
C25:3 (ECL = 26.45)	0.03	0.11	0.00	0.39	0.92
6-meC26	0.28	0.30	0.00	0.90	0.38
2-meC26, C27:2, C27:1	0.64	0.28	0.30	1.29	0.00
3-meC26	0.01	0.03	0.00	0.10	0.92
C27:1 (ECL = 26.85)	0.20	0.22	0.00	0.61	0.46
6,18-dimeC26	0.14	0.20	0.00	0.55	0.62
5,17-dimeC26	0.03	0.07	0.00	0.23	0.92
4,16-; 4,18-dimeC26; C26:3	0.04	0.09	0.00	0.28	0.77
C27	0.31	0.29	0.00	0.86	0.31
13-, 11-, 9-, 7-meC27; C27:2	1.99	0.60	1.18	3.34	0.00
C27:2 (ECL = 27.50)	0.09	0.34	0.00	1.22	0.92
5-meC27	0.35	0.29	0.00	1.02	0.15
2-meC27	0.01	0.02	0.00	0.07	1.00
3-meC27	0.13	0.12	0.00	0.36	0.38
5,17-dimeC27	1.67	1.91	0.00	5.19	0.23
C27:3 (ECL = 27.85)	0.50	0.84	0.00	3.09	0.38
C27:3 (ECL = 28.09)	0.23	0.37	0.00	0.88	0.69
C29	0.05	0.12	0.00	0.38	0.85
13,17-; 11,15-dimeC35	0.01	0.05	0.00	0.19	0.92
5,17-dimeC35	0.21	0.20	0.00	0.63	0.38
5,9,17-trimeC35	0.01	0.03	0.00	0.12	0.92
6,18-; 5,17-dimeC36	0.28	0.21	0.00	0.65	0.23
17-, 15-, 13-, 11-meC37	1.19	0.92	0.34	2.72	0.00
13,17-; 11,15-dimeC37	0.09	0.14	0.00	0.43	0.62
7,17-dimeC37	0.02	0.06	0.00	0.21	0.92
5,17-dimeC37	3.97	1.27	1.68	5.95	0.00
5,9,17-trimeC37	0.25	0.27	0.00	0.94	0.31
12-, 11-meC38	0.42	0.39	0.00	1.13	0.23
6,18-; 5,17-dimeC38	0.56	0.39	0.00	1.39	0.15
15-, 13-, 11-meC39	2.19	0.67	1.32	3.47	0.00
13,17-dimeC39	0.96	0.30	0.41	1.41	0.00
7,17-dimeC39	0.01	0.03	0.00	0.12	0.92
5,17-dimeC39	2.54	1.30	0.98	4.68	0.00
5,9,17-trimeC39	0.05	0.12	0.00	0.37	0.85
12-, 11-meC40	0.04	0.09	0.00	0.28	0.85
5,17-dimeC40	0.13	0.30	0.00	1.01	0.77
15-, 13-, 11-meC41	0.44	0.28	0.00	0.85	0.15
13,17-dimeC41	0.62	0.42	0.00	1.10	0.23
5,17-dimeC41	2.03	2.59	0.41	9.69	0.00
15-, 13-, 11-meC43	0.06	0.15	0.00	0.52	0.77
13,17-dimeC43	0.17	0.27	0.00	0.62	0.69
5,17-dimeC43	0.37	0.46	0.00	1.61	0.31

[a] Hydrocarbons that coelute are listed together in the table.

specific mixtures of cuticular hydrocarbons in termites is extensive (Page et al. 2002, and references therein). Characterization of cuticular hydrocarbons often leads to subsequent morphological, biological, behavioral, or other chemical studies that clarify taxonomic questions (Haverty et al. 1988, 1991, 1999a,b, 2003; Haverty and Thorne 1989; Thorne and Haverty 1989; Thorne et al. 1993; Haverty and Nelson 1997; Delphia et al. 2003; Copren et al. 2005).

Reticulitermes spp. seem to possess three lineages whose distributions are not confined to a particular

Table 5. Percentage of total hydrocarbon from workers of *Reticulitermes* phenotype AZ-C

Hydrocarbon[a]	Mean (n = 13)	SD (%)	Min.	Max.	Prop. <0.1%
C24	0.03	0.11	0.00	0.40	0.92
2-meC24, C25:2, C25:1, 3-meC24	0.34	1.21	0.00	4.39	0.92
C25	0.94	1.86	0.00	6.95	0.23
13-, 11-, 9-, 7-meC25	0.04	0.16	0.00	0.57	0.92
2-meC25	0.28	0.61	0.00	2.24	0.54
3-meC25	1.93	1.15	0.64	4.79	0.00
C26	0.30	0.18	0.00	0.56	0.15
2-meC26, C27:2, C27:1	9.00	3.94	4.54	18.34	0.00
C27	3.20	0.98	1.43	4.52	0.00
C27:1 (ECL = 27.14)	0.10	0.15	0.00	0.48	0.62
13-, 11-, 9-, 7-meC27; C27:2	0.77	0.45	0.00	1.63	0.08
C27:2 (ECL = 27.50)	0.12	0.45	0.00	1.61	0.92
5-meC27	0.87	0.32	0.42	1.39	0.00
2-meC27	2.30	0.55	0.90	3.06	0.00
3-meC27	3.88	1.03	1.64	6.27	0.00
5,17-dimeC27	0.29	0.23	0.00	0.56	0.31
C28	0.48	0.21	0.00	0.77	0.08
C29:2 (ECL = 28.50)	2.85	1.52	1.03	6.10	0.00
C29:1 (ECL = 28.70)	26.33	2.94	21.81	30.65	0.00
C29	1.09	0.36	0.26	1.68	0.00
C29:2 (ECL = 29.10)	0.44	0.29	0.00	0.85	0.23
C29:1 (ECL = 29.15)	0.26	0.25	0.00	1.03	0.15
15-, 13-, 11-, 9-, 7-meC29; C29:2	2.38	0.77	1.26	4.01	0.00
5-meC29	0.65	0.16	0.37	0.90	0.00
2-meC29	0.33	0.16	0.00	0.48	0.15
3-meC29	1.11	0.25	0.69	1.50	0.00
5,17-dimeC29	1.91	0.52	1.31	2.84	0.00
C30	0.08	0.10	0.00	0.25	0.54
C31:2 (ECL = 30.40)	8.74	2.05	5.59	12.00	0.00
2-meC30; C31:1	0.55	0.40	0.00	1.53	0.15
C31:1 (ECL = 30.70)	2.33	0.50	1.88	3.79	0.00
C31	0.22	0.12	0.00	0.37	0.15
C31:2 (ECL = 31.10)	0.37	0.41	0.00	1.43	0.38
15-, 13-, 11-meC31; C31:2	4.18	1.89	0.81	7.79	0.00
3-meC31	0.10	0.11	0.00	0.29	0.54
5,17-dimeC31	1.74	0.91	0.68	3.52	0.00
C33:2 (ECL = 32.40)	6.47	1.94	4.51	10.72	0.00
5,17-dimeC32	0.25	0.29	0.00	0.85	0.46
C33	0.16	0.18	0.00	0.49	0.46
13-, 11-meC33	0.62	0.32	0.00	0.99	0.15
5,17-dimeC33	1.32	1.04	0.00	3.52	0.08
C35:2	1.68	0.54	1.17	2.94	0.00
6,18-; 5,17-dimeC34	0.06	0.12	0.00	0.35	0.77
5,17-dimeC35	0.33	0.39	0.00	1.24	0.31
C37:2	0.05	0.08	0.00	0.27	0.77
5,17-dimeC37	0.71	0.26	0.00	1.01	0.08
5,9,17-trimeC37	0.10	0.11	0.00	0.29	0.46
C39:3, C39:2	0.81	0.34	0.00	1.28	0.08
6,18-; 5,17-dimeC38	0.12	0.12	0.00	0.33	0.38
15-, 13-, 11-meC39	0.27	0.40	0.00	1.11	0.54
13,17-dimeC39	0.02	0.08	0.00	0.28	0.92
5,17-dimeC39	1.02	0.49	0.00	2.02	0.08
5,9,17-trimeC39	0.19	0.16	0.00	0.43	0.38
C41:2	1.18	0.47	0.30	1.72	0.00
15-, 13-, 11-meC41	0.06	0.15	0.00	0.52	0.85
5,17-dimeC41	2.02	0.62	0.54	2.78	0.00
C43:2	0.17	0.19	0.00	0.43	0.54
5,17-dimeC42	0.03	0.08	0.00	0.25	0.85
5,17-dimeC43	1.79	1.06	0.00	3.67	0.15
C45:2	0.02	0.08	0.00	0.28	0.92

[a] Hydrocarbons that coelute are listed together in the table.

Table 6. Percentage of total hydrocarbon from workers of *Reticulitermes* phenotype AZ-D

Hydrocarbon[a]	Mean (n = 3)	SD (%)	Min.	Max.	Prop. <0.1%
C23:1	0.14	0.24	0.00	0.42	0.67
C23	3.66	0.46	3.31	4.18	0.00
11-, 9-, 7-meC23	1.93	0.15	1.75	2.03	0.00
2-meC23	0.79	0.01	0.78	0.80	0.00
3-meC23	1.10	0.41	0.79	1.56	0.00
C24	1.44	0.36	1.21	1.86	0.00
12-, 11-, 10-, 9-meC24	1.95	0.14	1.80	2.05	0.00
2-meC24, C25:2, C25:1, 3-meC24	3.75	0.84	3.17	4.70	0.00
C25	6.79	1.79	5.21	8.73	0.00
13-, 11-, 9-, 7-meC25	18.12	1.41	17.07	19.73	0.00
C25:2 (ECL = 25.50)	3.18	0.82	2.64	4.12	0.00
11,15-dimeC25; 2-meC25	12.40	2.01	10.18	14.09	0.00
3-meC25	2.88	1.38	1.73	4.41	0.00
C25:3 (ECL = 25.98)	1.48	0.45	0.99	1.88	0.00
C25:3 (ECL = 26.07)	9.04	1.47	7.98	10.72	0.00
C25:3 (ECL = 26.30)	0.30	0.51	0.00	0.89	0.67
13-, 12-, 11-meC26	0.26	0.45	0.00	0.77	0.67
C25:3 (ECL = 26.45)	0.44	0.76	0.00	1.32	0.67
2-meC26, C27:2, C27:1	0.61	0.53	0.00	0.99	0.33
C27	0.15	0.26	0.00	0.45	0.67
C26:3 (ECL = 27.15)	0.18	0.31	0.00	0.53	0.67
13-, 11-, 9-, 7-meC27; C27:2	0.50	0.44	0.00	0.84	0.33
C27:2 (ECL = 27.50)	0.13	0.22	0.00	0.38	0.67
2-meC27	0.17	0.29	0.00	0.50	0.67
3-meC27	0.14	0.24	0.00	0.42	0.67
C27:3 (ECL = 27.85)	0.49	0.54	0.00	1.07	0.33
11-meC35	2.68	0.24	2.40	2.85	0.00
13,17-; 11,15-dimeC35	3.93	0.93	3.18	4.97	0.00
12-, 11-meC36	0.76	0.37	0.36	1.10	0.00
12,16-; 11,15-dimeC36	1.03	0.10	0.92	1.09	0.00
17-, 15-, 13-, 11-meC37	4.93	1.42	3.89	6.54	0.00
13,17-; 11,15-dimeC37	6.68	2.18	4.40	8.73	0.00
12-, 11-meC38	0.44	0.19	0.24	0.61	0.00
12,16-; 11,15-dimeC38	0.63	0.44	0.36	1.14	0.00
15-, 13-, 11-meC39	1.72	0.80	1.25	2.64	0.00
13,17-dimeC39	2.85	0.55	2.48	3.47	0.00
12,16-dimeC40	0.09	0.15	0.00	0.26	0.67
15-, 13-, 11-meC41	0.37	0.33	0.00	0.64	0.33
13,17-dimeC41	1.08	0.97	0.00	1.87	0.33
5,17-dimeC43	0.83	1.43	0.00	2.48	0.67

[a] Hydrocarbons that coelute are listed together in the table.

geographical region in the United States (Page et al. 2002). Cuticular hydrocarbon mixtures of lineage I have a preponderance of internally branched monomethylalkanes and 11,15-dimethylalkanes; lineage II is defined by a preponderance of 5-methylalkanes and 5,17-dimethylalkanes; and lineage III is characterized by a preponderance of olefins and a relative paucity of *n*-alkanes and methyl-branched alkanes. AZ-D is in lineage I; AZ-A, AZ-B, and NM-A are in lineage II; and AZ-C is in lineage III; AZ-C is completely different from any of the other southwestern *Reticulitermes* spp. (Page et al. 2002).

Cluster analysis of the samples from Arizona, New Mexico, Nevada, and Utah resulted in five major clusters. The AZ-C phenotype separated from all the other samples based on the abundance of C29:1 (Fig. 4). Curiously, a collection (UT033) from Grand County, UT, also falls in this cluster, extending the distribution of AZ-C phenotype north into Utah. The quantities of the isomeric mixture of 7-, 9-, 11-, and 13-meC27 and C27:2 separate phenotypes AZ-A, AZ-B, and AZ-D from samples characterized as NM-A and collected in Grand County, UT, and Jemez Springs, NM (Fig. 4; Table 2) These three samples from Utah and New Mexico (NM034, UT034, and UT038) are different

Table 7. Percentage of total hydrocarbon from workers of *Reticulitermes* phenotype NM-A

Hydrocarbon[a]	Mean (n = 3)	SD (%)	Min.	Max.	Prop. <0.1%
C23	0.05	0.04	0.00	0.07	1.00
2-meC23	0.09	0.03	0.06	0.12	0.67
C24	0.62	0.13	0.47	0.70	0.00
12-, 11-, 10-, 9-meC24	0.20	0.08	0.14	0.29	0.00
2-meC24, C25:2, C25:1, 3-meC24	7.00	0.34	6.64	7.31	0.00
C25	7.03	2.07	5.08	9.20	0.00
13-, 11-, 9-, 7-meC25	11.31	3.33	9.37	15.15	0.00
5-meC25	0.67	0.43	0.31	1.15	0.00
9,13-dimeC25; 2-meC25	3.84	0.38	3.41	4.11	0.00
3-meC25	7.58	0.52	7.17	8.16	0.00
5,15-; 5,17-dimeC25	0.51	0.26	0.35	0.81	0.00
C25:3 (ECL = 25.98)	2.14	1.39	0.81	3.59	0.00
C25:3 (ECL = 26.07)	0.68	0.36	0.27	0.96	0.00
13-, 12-, 11-meC26; C26:2	3.09	0.74	2.34	3.82	0.00
C25:3 (ECL = 26.45)	0.16	0.28	0.00	0.48	0.67
6-meC26	0.25	0.22	0.00	0.40	0.33
2-meC26, C27:2, C27:1	3.06	0.41	2.62	3.44	0.00
C27:1 (ECL = 26.85)	4.31	2.67	1.81	7.12	0.00
C27, C27:3	10.90	5.06	7.68	16.73	0.00
13-, 11-, 9-, 7-meC27; C27:2	18.96	5.19	13.50	23.84	0.00
C27:2 (ECL = 27.50)	0.68	0.68	0.00	1.36	0.33
5-meC27	0.32	0.56	0.00	0.97	0.67
2-meC27	0.41	0.04	0.37	0.44	0.00
3-meC27	0.44	0.11	0.31	0.52	0.00
5,17-dimeC27	3.06	0.91	2.08	3.89	0.00
C27:3 (ECL = 27.85)	1.08	0.77	0.49	1.95	0.00
C28	0.12	0.21	0.00	0.37	0.67
C27:3 (ECL = 28.09)	0.56	0.60	0.00	1.20	0.33
C29:3 (ECL = 29.00)	1.76	0.66	1.05	2.36	0.00
15-, 13-, 11-, 9-, 7-meC29; C29:2	0.41	0.38	0.00	0.75	0.33
C37:2 (ECL = 36.40)	0.84	0.81	0.17	1.74	0.00
17-, 15-, 13-, 11-meC37	0.15	0.25	0.00	0.44	0.67
7,17-dimeC37	0.07	0.13	0.00	0.22	0.67
5,17-dimeC37	0.31	0.42	0.00	0.79	0.33
C39:5, C39:4	1.40	1.00	0.50	2.47	0.00
C39:3, C39:2	2.52	0.60	1.85	3.03	0.00
6,18-; 5,17-dimeC38	0.04	0.08	0.00	0.13	0.67
15-, 13-, 11-meC39	0.52	0.60	0.00	1.17	0.33
13,17-dimeC39	0.32	0.13	0.18	0.44	0.00
5,17-dimeC39	0.32	0.41	0.00	0.78	0.33
C41:2	0.13	0.23	0.00	0.40	0.67
15-, 13-, 11-meC41	0.27	0.14	0.13	0.40	0.00
13,17-dimeC41	0.39	0.15	0.22	0.52	0.00
5,17-dimeC41	0.15	0.15	0.00	0.30	0.33
15-, 13-, 11-meC43	0.14	0.12	0.00	0.23	0.33
13,17-dimeC43	0.85	0.44	0.36	1.21	0.00
5,17-dimeC43	0.27	0.13	0.16	0.41	0.00

[a] Hydrocarbons that coelute are listed together in the table.

enough from the AZ-A, AZ-B, and AZ-D phenotypes to represent yet another taxon of *Reticulitermes.* The internally branched monomethyl C25 separates the AZ-B phenotype from the AZ-A and AZ-D phenotypes (Fig. 4). The samples in the AZ-B cluster range over most of Arizona from Fredonia, North Rim of the Grand Canyon, Heber, and as far south as Tucson and Sabino Canyon. This cluster also includes samples from southwestern Utah (UT002) and east central Nevada (NV-003). The internally branched dimethylalkane, 9,13-dimeC25, coeluting with 2-meC25, divides the AZ-A and AZ-D clusters. The samples in the AZ-A cluster were collected in east central Arizona, and one sample was from the Chaco Cultural National Historic Park in northern New Mexico (NM035). Phenotype AZ-D has only been collected once (AZ3) in Arizona; however, it shares a cuticular hydrocarbon mixture with samples collected from Mt. Charleston near Las Vegas, NV (NV-005 and NV-008), and it is very similar to that of *R. hesperus* from northern California (Haverty et al. 2003, Copren et al. 2005). These distinctions allow us to construct a diagnostic key to species based on cuticular hydrocarbons (Tables 8 and 9).

Table 8. Percentage of total hydrocarbon for diagnostic hydrocarbons from workers of *Reticulitermes* from five cuticular hydrocarbon phenotypes from Arizona and adjacent states

Hydrocarbon[a]	AZ-A	AZ-B	AZ-C	AZ-D	NM-A
13-, 11-, 9-, 7-meC25	15.36	28.40	0.04	18.12	11.31
C25:2	0.00	0.00	0.00	3.18	0.00
5-meC25	1.84	2.41	0.00	0.00	0.67
11,15-dimeC25; 2-meC25	4.72[b]	4.07[b]	0.28[b]	12.40	3.84[b]
C25:3	2.11	1.51	0.00	0.30	2.14
C25:3	1.47	2.05	0.00	9.04	0.68
C27:1	2.25	0.20	0.00	0.00	4.31
C27, 27:3	1.79	0.31[c]	3.20[c]	0.15[c]	10.90
13-, 11-, 9-, 7-meC27; C27:2	7.79	1.99	0.77	0.50	18.96
5,17-dimeC27	7.32	1.67	0.29	0.00	3.00
C29:2	0.00	0.00	2.85	0.00	0.00
C29:1	0.00	0.00	26.33	0.00	0.00
C31:2	0.00	0.00	8.74	0.00	0.00
15-, 13-, 11-meC31; C31:2	0.00	0.00	4.18	0.00	0.00
C33:2	0.00	0.00	6.47	0.00	0.00
11-meC35	0.00	0.00	0.00	2.68	0.00
13,17-; 11,15-dimeC35	0.00	0.01	0.00	3.93	0.00
17-, 15-, 13-, 11-meC37	0.42	1.19	0.00	4.93	0.15
13,17-; 11,15-dimeC37	0.00	0.09	0.00	6.68	0.00
5,17-dimeC37	1.40	3.97	0.71	0.00	0.31
C39:5, C39:4	1.53	0.00	0.00	0.00	1.40
C39:3, C39:2	3.77	0.00	0.81	0.00	2.52
5,17-dimeC39	1.75	2.54	1.02	0.00	0.32
5,17-dimeC41	0.54	2.03	2.02	0.00	0.15
15-, 13-, 11-meC43	0.14	0.06	1.79	0.00	0.14

[a] Hydrocarbons that coelute are listed together in the table.
[b] Only 2-meC25 found in this peak for this phenotype.
[c] Only C27 found in this peak for this phenotype.

Biogeography of *Reticulitermes* in Arizona. Because we tried to collect more than one colony at each stop, we had 13 stops at which we collected two different hydrocarbon phenotypes (Tables 1 and 2). AZ-A was not common; the few samples we collected were all at the higher elevations (2,000–2,250 m) in Arizona (Figs. 5 and 6). We had one stop where AZ-A was collected with AZ-B (Second Mesa) and one stop with AZ-C (Junction of AZ 277 and 377). AZ-B was very common and was found throughout Arizona from Fairbank (≈1,300 m) to Jacob Lake (≈2,600 m). This phenotype also was found in eastern Nevada and southwestern Utah. AZ-C was sympatric with AZ-B over most of the distribution of the latter. We made nine collections that provided samples of both AZ-B and AZ-C (Table 1). AZ-C tended to occur at higher elevations (>1,500 m) on the desert islands of southeastern Arizona, such as the Santa Catalina, Santa Rita, Chiricahua, and Pinaleno mountains, whereas AZ-B was collected at lower elevations (<1,250 m), usually associated with a riparian area in the southeastern corner of the state. AZ-D was only collected by us at

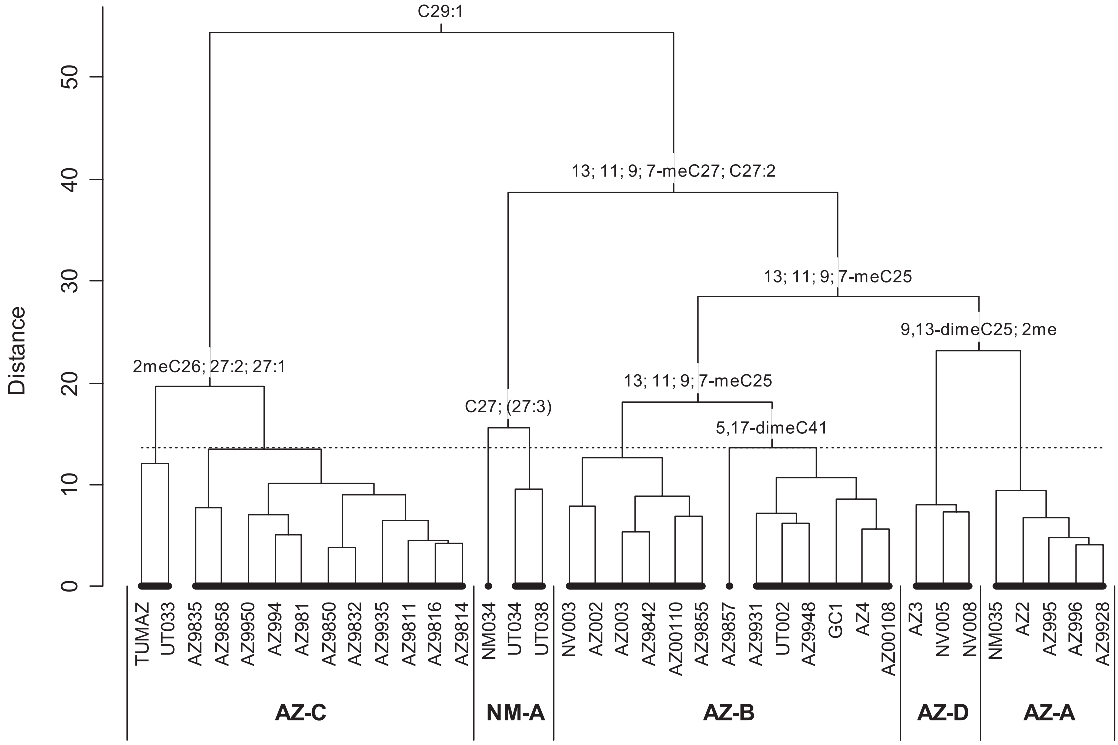

Fig. 4. Dendrogram from cluster analysis based on Euclidean distance of hydrocarbons extracted from 37 samples of workers of *Reticulitermes* spp. from Arizona, Nevada, New Mexico, and Utah.

one location in Arizona (16.1 km east of Jacob Lake); a collection of AZ-B was made only 3.2 km west of this location, albeit ≈200 m higher in elevation.

Uva et al. (2004) noted that most European scientists assume that the classification of termites is definitive and have been identifying samples based on geographic origin alone. Some *Reticulitermes* samples showing phenotypical differences from congeneric European species have been classified as *R. lucifigus* simply because they were collected in Italy (Uva et al. 2004). We suspect a similar situation occurs in the United States. Acceptance of the Snyder (1949, 1954) and Weesner (1970) reports on the distribution of *Reticulitermes* facilitates easy identification to species: if it occurs in Arizona, Nevada, New Mexico, or Utah, it can only be *R. tibialis.* Furthermore, we know of no studies of *Reticulitermes* in California since 1934 (other than our own) that use a species diagnosis

Table 9. Dichotomous key to the cuticular hydrocarbon phenotypes of *Reticulitermes* from Arizona and adjacent states based on diagnostic hydrocarbons

Character	Phenotype
1. C29:1 present	Phenotype AZ-C or *Reticulitermes tumiceps*
C29:1 absent	2
2. 5,17-dimeC27/37/39/41 absent; 11-meC35 and 11,15-dimeC35 present	Phenotype AZ-D or *Reticulitermes hesperus*
5,17-dimeC27/37/39/41 present; 11-meC35 and 11,15-dimeC35 absent	3
3. C39:X absent	Phenotype AZ-B
C39:X present	4
4. 13-, 11-, 9-, 7-meC27; C27:2 > 12% and C27 + C27:3 > 5%	Phenotype NM-A
13-, 11-, 9-, 7-meC27; C27:2 < 12% and C27 + C27:3 < 5%	Phenotype AZ-A

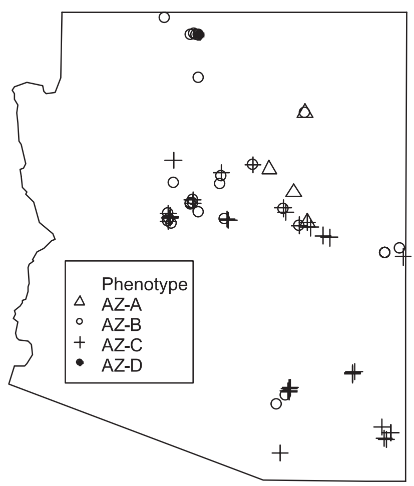

Fig. 5. Distribution of *Reticulitermes* of four cuticular hydrocarbon phenotypes (AZ-A, AZ-B, AZ-C, and AZ-D) in Arizona.

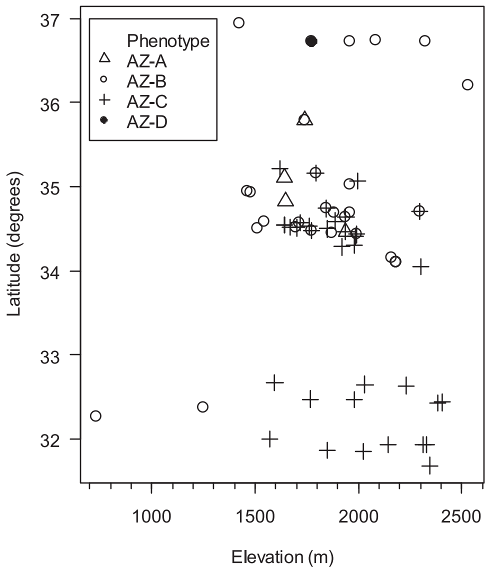

Fig. 6. Elevation and latitude of *Reticulitermes* of four cuticular hydrocarbon phenotypes (AZ-A, AZ-B, AZ-C, and AZ-D) in Arizona.

other than *R. hesperus.* Hopefully, our study reported here will instill caution in identifying *Reticulitermes* to species based solely on geography.

Taxonomic Implications of Cuticular Hydrocarbons of *Reticulitermes* in Arizona. At first, it may seem that the *Reticulitermes* samples collected in Arizona since the days of Banks and Snyder (1920) are a single, morphologically variable species. Now we know that these *Reticulitermes* include four phenotypes, some with sympatric distributions and others with elevationally disjunct distributions. Until a detailed, modern morphological study is completed, these phenotypes might be considered sibling species. Variations in ecology or behavior are usually the first indications of sibling species (Futuyma 1998), and we hope that morphological, behavioral, and genetic differences will be found later by which they can be distinguished. The evidence is mounting that these *Reticulitermes* from Arizona comprise four species. They have four distinct states (i.e., cuticular hydrocarbon phenotypes AZ-A, AZ-B, AZ-C, and AZ-D), but no intermediates.

We think, and have so stated, that existing keys to species of *Reticulitermes* are grossly inadequate and give a false sense of confidence in identifying species (Haverty et al. 1996, 1999c; Haverty and Nelson 1997; Nelson et al. 2001; Copren et al. 2005). Weesner (1970) was one of the first to warn the scientific community that *Reticulitermes*. . . "is woefully in need of a critical taxonomic study . . . soldiers are extremely variable . . . alates are also variable. . . ". She seemed to be especially puzzled by *R. tibialis* noting that "flights of *R. tibialis* occur over a wide span of the year, primarily during the fall, winter and spring. . . . Collections of *R. tibialis* from Texas are extremely variable." We should not lose sight of the fact that the type locality of *R. tibialis* is Beeville, TX, not anywhere in Arizona (Snyder 1949).

Reports concerning the place of *R. tibialis* in the phylogeny of *Reticulitermes* add further confusion. The mitochondrial DNA (mtDNA) COII sample in GenBank (AF525355) for *R. tibialis* is reported to occur in Cochise County, AZ (Austin et al. 2002). This GenBank sample has been associated with undescribed species of *Reticulitermes* from Catalina Island, CA (GenBank AF525342), and from the eastern slope of the Sierra Nevada in California (GenBank AY623435 and AY623476), as well as *Reticulitermes grassei* Clément (GenBank AF525327) (Austin et al. 2002, 2004; Copren et al. 2005). Using the mtDNA 16S gene, *R. tibialis* (GenBank AY25736) also has been associated with a sample from San Bernardino, CA (GenBank AY25737) (Szalanski et al. 2003). The only samples that we have collected from Cochise County, AZ, were hydrocarbon phenotype AZ-C, although we do not have any samples from lower elevations where we might find AZ-B. So, it is possible that *R. tibialis* does occur in Arizona and that it equates with AZ-B. However, until we can associate a cuticular hydrocarbon phenotype or an mtDNA genotype with collections from the type locality, Beeville, TX, caution is warranted in determining which cuticular hydrocarbon phenotype or genotype is *R. tibialis.* Furthermore, the keys are not trustworthy (Copren et al. 2005).

Cuticular hydrocarbon mixtures can be used to discriminate insect taxa. Like most features, cuticular hydrocarbon mixtures are polygenically inherited (Coyne et al. 1994, Dallerac et al. 2000, Takahashi et al. 2001). They have the utility for determining phylogenetic relationships where they are independent characters with discrete states and represent a hierarchical distribution of shared, derived characters (Page et al. 2002). The association of cuticular hydrocarbon phenotypes and mtDNA haplotypes demonstrates that they are useful in separating known species, determining new species, and provide further support for the species-specific nature of cuticular hydrocarbon phenotypes (Howard and Blomquist 1982, Jenkins et al. 2000, Copren et al. 2005). Foster et al. (2004) assert that molecular or chemical characters provide a better means of identifying termite workers or pseudergates to species.

Brand (1978) stated that all available evidence, including chemical data, should be taken into account in describing a taxon and suggested that the biosynthetic homology of chemical characters provides a closer look at genetic relationships than does the similarity of morphological characters. Chemical variation certainly seems as likely to affect behavior as would variation in morphology. This suggests that chemical characters, such as cuticular hydrocarbons and soldier defense secretions, are ideal tools for understanding the evolutionary relationships of termites (Nelson et al. 2001). Takematsu and Yamaoka (1999) identified nine cuticular hydrocarbon phenotypes of *Reticulitermes* occurring in Japan and neighboring countries. Each of these nine taxa had unique compounds that could be used to separate them. By sorting on chemical factors Takematsu (1999) was able to find new morphological characters for separating species.

The most dramatic revelation in our survey of the cuticular hydrocarbons of *Reticulitermes* from Arizona is the consistency of the unique hydrocarbon mixture of the samples from the mountain islands in southeastern Arizona. Collections (topotypes) from the type locality of the original, single collection named *R. tumiceps* Banks (Banks and Snyder 1920) are phenotype AZ-C, which is completely different from any of the other southwestern *Reticulitermes* (Page et al. 2002). Only this phenotype has been collected from the vicinity of Stratton Camp, AZ, at 1,900–2,250 m on the north side of the Santa Catalina Mountains, Pima County, AZ, north of Tucson. Thus we argue that *R. tumiceps* is a valid taxon and should be resurrected. AZ-D is a sister taxon to CA-A and CA-A′ (Page et al. 2002), which has been designated the cuticular hydrocarbon phenotype of *R. hesperus* (Haverty et al. 2003). Therefore, it is likely that *R. hesperus* occurs in Arizona but is somewhat rare.

Two of the phenotypes from Arizona (AZ-A and AZ-B) and one from New Mexico and Utah (NM-A) are similar to one from California (CA-D), an undescribed species (Haverty and Nelson 1997, Haverty et al. 1999c) and are part of lineage II (Page et al. 2002). AZ-A is more similar to AZ-D or *R. hesperus* than to AZ-B or NM-A. AZ-A was collected only in the northeastern quarter of Arizona. AZ-B is very widespread in distribution, is also more variable chemically, and may be the most common phenotype or species of *Reticulitermes* in Arizona. These three phenotypes (AZ-A, AZ-B, and NM-A) were considered to be closely related by Page et al. (2002) based on phylogenetic analyses of the cuticular hydrocarbons, yet distinct taxa. NM-A has not yet been collected in Arizona, but it represents a distinct taxon found thus far only in New Mexico and Utah.

In summary, sympatric distributions of termite populations with distinct cuticular hydrocarbon and soldier defense secretion mixtures (Haverty and Nelson 1997; Haverty et al. 1999c, 2003; Nelson et al. 2001; Page et al. 2002; Copren et al. 2005) convince us that AZ-A, AZ-B, AZ-C, and AZ-D represent different species. AZ-D is not common in Arizona and likely represents an incursion of *R. hesperus* into northeastern Arizona. AZ-C is a unique, valid species and should be the phenotype describing *R. tumiceps* originally proposed by Banks and Snyder (1920) and later synonymized with *R. tibialis* by Snyder (1949). AZ-B is widely distributed and common in Arizona and could be the phenotype representing *R. tibialis.* AZ-A was found less often and is most similar to AZ-D or *R. hesperus.* It has been found only in the higher elevations of Arizona and New Mexico and also could represent *R. tibialis.* Finally, a fifth phenotype, NM-A, which has not yet been found in Arizona but has been collected in New Mexico and Utah, clearly represents a distinct taxon. As with AZ-A and AZ-B, this phenotype might be *R. tibialis.* Thus, we are hesitant to assign a cuticular hydrocarbon phenotype to the arid lands termite, *R. tibialis.* Characterization of the cuticular hydrocarbons of topotypes could solve this mystery and facilitate assigning the genotype to *R. tibialis.*

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References Cited

Austin, J. W., A. L. Szalanski, P. Uva, A.-G. Bagnères, and A. Kence. 2002. A comparative genetic analysis of the subterranean termite genus *Reticulitermes* (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Am. 95: 753–760.

Austin, J. W., A. L. Szalanski, and B. Cabrera. 2004. Phylogenetic analysis of the subterranean termite family Rhinotermitidae (Isoptera) by using the mitochondrial cytochrome oxidase II gene. Ann. Entomol. Soc. Am. 97: 548–555.

Banks, F. A. 1946. Species distinction in *Reticulitermes* (Isoptera: Rhinotermitidae). M.S. thesis, University of Chicago, Chicago, IL.

Banks, N., and T. E. Snyder. 1920. A revision of the Nearctic termites. Bull. U.S. Natl. Mus. 108: 1–228.

Blomquist, G. J., and J. W. Dillwith. 1985. Cuticular lipids, pp. 117–154. *In* G. A. Kerkut and L. I. Gilbert [eds.], Comprehensive insect physiology, biochemistry and pharmacology, vol. 3. Integument, respiration and circulation. Pergamon, Oxford, United Kingdom.

Blomquist, G. J., D. R. Nelson, and M. de Renobales. 1987. Chemistry, biochemistry, and physiology of insect cuticular lipids. Arch. Insect Biochem. Physiol. 6: 227–265.

Brand, J. M. 1978. Fire and venom alkaloids: their contribution to chemosystematics and biochemical evolution. Biochem. Syst. Ecol. 6: 337–340.

Clément, J.-L., A.-G. Bangères, P. Uva, L. Wilfert, A. Quintana, J. Reinhard, and S. Dronnet. 2001. Biosystematics of *Reticulitermes* termites in Europe: morphological, chemical and molecular data. Insectes Soc. 48: 202–215.

Copren, K. A., L. J. Nelson, E. L. Vargo, and M. I. Haverty. 2005. Phylogenetic analyses of mtDNA sequences corroborate taxonomic designations based on cuticular hydrocarbons in subterranean termites. Mol. Phylogenet. Evol. 35: 689–700.

Coyne, J. A., A. P. Crittenden, and K. Mah. 1994. Genetics of a pheromonal difference contributing to reproductive isolation in *Drosophila.* Science (Wash., D.C.) 265: 1461–1464.

Dallerac, R., C. Labeur, J.-M. Jallon, D. C. Knipple, W. L. Roelofs, and C. Wicker-Thomas. 2000. A $\Delta 9$ desaturase gene with a different substrate specificity is responsible for the cuticular diene hydrocarbon polymorphism in *Drosophila melanogaster.* Proc. Natl. Acad. Sci. U.S.A. 97: 9449–9454.

Delphia, C. M., K. A. Copren, and M. I. Haverty. 2003. Agonistic behavior between individual worker termites from three cuticular hydrocarbon phenotypes of *Reticu-*

litermes (Isoptera: Rhinotermitidae) from northern California. Ann. Entomol. Soc. Am. 96: 585–593.

Foster, B. T., A. I. Cognato, and R. E. Gold. 2004. DNA-based identification of the eastern subterranean termite, *Reticulitermes flavipes* (Isoptera: Rhinotermitidae). J. Econ. Entomol. 97: 95–101.

Futuyma, D. J. 1998. Evolutionary biology, 3rd ed. Sinauer, Inc., Sunderland, MA.

Getty, G. M., M. I. Haverty, K. A. Copren, and V. R. Lewis. 2000a. Response of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in northern California to baiting with hexaflumuron with Sentricon Termite Colony Elimination System. J. Econ. Entomol. 93: 1498–1507.

Getty, G. M., M. I. Haverty, and V. R. Lewis. 2000b. Agonistic behavior between recently collected and laboratory cultured *Reticulitermes* spp. (Isoptera: Rhinotermitidae) from northern California. Pan-Pac. Entomol 76: 243–250.

Haverty, M. I., and L. J. Nelson. 1997. Cuticular hydrocarbons of *Reticulitermes* (Isoptera: Rhinotermitidae) from northern California indicate undescribed species. Comp. Biochem. Physiol. 118B: 869–880.

Haverty, M. I., and W. L. Nutting. 1976. Environmental factors affecting the geographical distribution of two ecologically equivalent termite species in Arizona. Am. Midl. Nat. 95: 20–27.

Haverty, M. I., and B. L. Thorne. 1989. Agonistic behavior correlated with hydrocarbon phenotypes in dampwood termites, *Zootermopsis* (Isoptera: Termopsidae). J. Insect Behav. 2: 523–543.

Haverty, M. I., L. J. Nelson, and M. Page. 1991. Preliminary investigations of the cuticular hydrocarbons from North American *Reticulitermes* and tropical and subtropical *Coptotermes* (Isoptera: Rhinotermitidae) for chemotaxonomic studies. Sociobiology 19: 51–76.

Haverty, M. I., M. Page, L. J. Nelson, and G. J. Blomquist. 1988. Cuticular hydrocarbons of dampwood termites, *Zootermopsis:* intra- and intercolony variation and potential as taxonomic characters. J. Chem. Ecol. 14: 1035–1058.

Haverty, M. I., B. T. Forschler, and L. J. Nelson. 1996. An assessment of the taxomony of *Reticulitermes* (Isoptera: Rhinotermitidae) from the southeastern United States based on cuticular hydrocarbons. Sociobiology 28: 287–318.

Haverty, M. I., K. A. Copren, G. M. Getty, and V. R. Lewis. 1999a. Agonistic behavior and cuticular hydrocarbon phenotypes of colonies of *Reticulitermes* (Isoptera: Rhinotermitidae) from northern California. Ann. Entomol. Soc. Am. 92: 269–277.

Haverty, M. I., G. M. Getty, K. A. Copren, and V. R. Lewis. 1999b. Seasonal foraging and feeding behavior of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in a wildland and a residential location in northern California. Environ. Entomol. 28: 1077–1084.

Haverty, M. I., L. J. Nelson, and B. T. Forschler. 1999c. New cuticular hydrocarbon phenotypes of *Reticulitermes* (Isoptera: Rhinotermitidae) from the United States. Sociobiology 34: 1–21.

Haverty, M. I., G. M. Getty, K. A. Copren, and V. R. Lewis. 2000. Size and dispersion of colonies of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in a wildland and a residential location in northern California. Environ. Entomol. 29: 241–249.

Haverty, M. I., G. M. Getty, L. J. Nelson, and V. R. Lewis. 2003. Flight phenology of sympatric populations of *Reticulitermes* (Isoptera: Rhinotermitidae) in northern California: disparate flight intervals indicate reproductive isolation among cuticular hydrocarbon phenotypes. Ann. Entomol. Soc. Am. 96: 828–833.

Haverty, M. I., R. J. Woodrow, L. J. Nelson, and J. K. Grace. 2005. Identification of termite species by the hydrocarbons in their feces. J. Chem. Ecol. 31: 2119–2151.

Howard, R. W. 1993. Cuticular hydrocarbons and chemical communication, pp. 177–226. *In* D. W. Stanley-Samuelson and D. R. Nelson [eds.]. Insect lipids: chemistry, biochemistry, and biology. University of Nebraska Press, Lincoln, NE.

Howard, R. W., and G. J. Blomquist. 1982. Chemical ecology and biochemistry of insect hydrocarbons. Annu. Rev. Entomol. 27: 149–172.

Jenkins, T. M., M. I. Haverty, C. J. Basten, L. J. Nelson, M. Page, and B. T. Forschler. 2000. Correlation of mitochondrial haplotypes with cuticular hydrocarbon phenotypes of sympatric *Reticulitermes* species from the southeastern United States. J. Chem. Ecol. 26: 1525–1542.

Kaib, M., R. Brandl, and R.K.N. Bagine. 1991. Cuticular hydrocarbon profiles: a valuable tool in termite taxonomy. Naturwissenschaften 78: 176–179.

Light, S. F. 1927. A new and more exact method of expressing important specific characters of termites. Univ. Calif. Publ. Entomol. 4: 75–88.

Light, S. F. 1934. The termite fauna of North America with special reference to the United States, pp. 127–135. *In* C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe [eds.], Termites and termite control, 2nd ed. University of California Press, Berkeley, CA.

Miller, E. M. 1949. A handbook of Florida termites. University of Miami Press, Coral Gables, FL.

Nelson, L. J., L. G. Cool, B. T. Forschler, and M. I. Haverty. 2001. Correspondence of soldier defense secretion mixtures with cuticular hydrocarbon phenotypes for chemotaxonomy of the termite genus *Reticulitermes* in North America. J. Chem. Ecol. 27: 1449–1479.

Nutting, W. L. 1990. Insecta: Isoptera, pp. 997–1032. *In* D. L. Dindal [ed.], Soil biology guide. Wiley, New York.

Page, M., L. J. Nelson, M. I. Haverty, and G. J. Blomquist. 1990a. Cuticular hydrocarbons of eight species of North American cone beetles, *Conophthorus* Hopkins. J. Chem. Ecol. 16: 1173–1198.

Page, M., L. J. Nelson, M. I. Haverty, and G. J. Blomquist. 1990b. Cuticular hydrocarbons as chemotaxonomic characters for bark beetles: *Dendroctonus ponderosae, D. jeffreyi, D. brevicomis,* and *D. frontalis* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 83: 892–901.

Page, M., L. J. Nelson, B. T. Forschler, and M. I. Haverty. 2002. Cuticular hydrocarbons suggest three lineages in *Reticulitermes* (Isoptera: Rhinotermitidae) from North America. Comp. Biochem. Physiol. B. 131: 305–324.

Pickens, A. L. 1934a. The biology and economic significance of the western subterranean termite, *Reticulitermes hesperus,* pp. 157–183. *In* C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe [eds.], Termites and termite control, 2nd ed. University of California Press, Berkeley, CA.

Pickens, A. L. 1934b. The barren-lands subterranean termite, *Reticulitermes tibialis,* pp. 184–186. *In* C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe [eds.], Termites and termite control, 2nd ed. University of California Press, Berkeley, CA.

Pomonis, J. G., C. F. Fatland, D. R. Nelson, and R. G. Zaylskie. 1978. Insect hydrocarbons. Corroboration of structure by synthesis and mass spectrometry of mono- and dimethylalkanes. J. Chem. Ecol. 4: 27–38.

R Development Core Team. 2004. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (http://www.R-project.org).

Scheffrahn, R. H., and N.-Y. Su. 1994. Keys to soldier and winged adult termites (Isoptera) of Florida. Fla. Entomol. 77: 460–474.

Snyder, T. E. 1949. Catalog of the termites (Isoptera) of the world. Smithson. Misc. Collect. 112: 1–490.

Snyder, T. E. 1954. Order Isoptera. The termites of the United States and Canada. National Pest Control Assoc., New York.

Szalanski, A. L., J. W. Austin, and C. B. Owens. 2003. Identification of *Reticulitermes* species (Isoptera: Reticulitermatidae) from south central United States by PCR-RFLP. J. Econ. Entomol. 96: 1514–1519.

Takahashi, A., S.-C. Tsaur, J. A. Coyne, and C.-L. Wu. 2001. The nucleotide changes governing cuticular hydrocarbon variation and their evolution in *Drosophila melanogaster.* Proc. Natl. Acad. Sci. U.S.A. 98: 3920–3925.

Takematsu, Y. 1999. The genus *Reticulitermes* (Isoptera: Rhinotermitidae) in Japan, with description of a new species. Entomol. Sci. 2: 231–243.

Takematsu, Y., and R. Yamaoka. 1999. Cuticular hydrocarbons of *Reticulitermes* (Isoptera: Rhinotermitidae) in Japan and neighboring countries as chemotaxonomic characters. Appl. Entomol. Zool. 34: 179–188.

Thorne, B. L. 1999. Biology of subterranean termites of the genus *Reticulitermes,* pp. 1–30. *In* B. L. Thorne and B. T. Forschler [contributors], NPMA research report on subterranean termites. National Pest Management Association, Inc., Dunn Loring, VA.

Thorne, B. L., and M. I. Haverty. 1989. Accurate identification of *Zootermopsis* species (Isoptera: Termopsidae) based on a mandibular character of nonsoldier castes. Ann. Entomol. Soc. Am. 82: 262–266.

Thorne, B. L., M. I. Haverty, M. Page, and W. L. Nutting. 1993. Distribution and biogeography of the North American termite genus *Zootermopsis* (Isoptera: Termopsidae). Ann. Entomol. Soc. Am. 86: 532–544.

Uva, P., J.-L. Clément, J. W. Austin, J. Aubert, V. Zaffagnini, A. Quintana, and A.-G. Bagnères. 2004. Origin of a new *Reticulitermes* termite (Isoptera: Rhinotermitidae) inferred from mitochondrial and nuclear DNA data. Mol. Phylogenet. Evol. 30: 344–353.

Weesner, F. M. 1965. The termites of the United States. A handbook. The National Pest Control Association, Elizabeth, NJ.

Weesner, F. M. 1970. Termites of the Nearctic Region, pp. 477–525. *In* K. Krishna and F. M. Weesner [eds.], Biology of Termites, vol. II. Academic, New York.

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Appendix. Localities of *Reticulitermes* specimens in the Nutting Collection in the Entomology Museum of the University of Arizona

County	Collection locality	Date	Collector	Elevation (m)	Latitude (°N)	Longitude (°W)
Apache	12.2 km N Alpine on US 180	04/19/87	W.L. Nutting	2,417	33.93181	109.18693
Apache	AZ-Rt. 61 SW of Concho	08/16/56	W.L. Nutting	1,826	34.47738	109.60708
Apache	Canyon de Chelly @ Ledge Ruins	Unknown	W.L. Nutting	1,717	36.15108	109.48113
Apache	Canyon de Chelly National Monument	04/23/77	W.L. Nutting	1,717	36.15108	109.48113
Apache	Canyon del Muerto, near Chinle	04/21/73	W.L. Nutting	1,763	36.16143	109.42587
Apache	Chuska Mts., E of Lukachukai	09/07/70	R.C.A. Rice	2,608	36.42338	109.10525
Apache	Lupton	11/11/59	Unknown	1,909	35.34934	109.06461
Apache	Sanders	08/21/76	Travisano	1,785	35.21703	109.33561
Apache	St. Johns	08/06/58	W.L. Nutting	1,739	34.50655	109.36275
Cochise	1.6 km N of San Simon	01/20/62	W.L. Nutting	1,099	32.26883	109.22955
Cochise	6.4 km W of Willcox	09/03/58	W.L. Nutting	1,275	32.25332	109.8926
Cochise	Ash Canyon, Huachuca Mts.	06/10/66	F.G. Werner	1,779	31.3715	110.26228
Cochise	Benson	03/23/72	R. Robinetti	1,091	31.96984	110.29581
Cochise	Carr Canyon, Huachuca Mts.	08/06/56	R. Willey	1,991	31.40619	110.34631
Cochise	Carr Canyon, Huachuca Mts.	04/09/79	W.L. Nutting	1,991	31.40619	110.34631
Cochise	Carr Canyon, Huachuca Mts.	04/04/83	S.C. Burne	1,991	31.40619	110.34631
Cochise	Cave Creek Canyon, Chiricahua Mts.	03/29/70	J.F. Burger	1,549	31.89015	109.16813
Cochise	Chiricahua National Monument	07/05/56	R. Willey	1,649	32.00569	109.35574
Cochise	Cochise	02/01/87	W.L. Nutting	1,283	32.11464	109.92283
Cochise	Fairbank @ San Pedro River	04/26/87	W.L. Nutting	1,189	31.71541	110.17818
Cochise	Forest Camp at peak near Rucker Canyon, Chiricahua Mts.	08/10/67	W.L. Nutting	1,888	31.78512	109.30265
Cochise	Forest Camp in vicinity of Rucker Canyon, Chiricahua Mts.	08/09/67	W.L. Nutting	1,811	31.87105	109.23421
Cochise	Guadelupe Canyon	10/19/57	W.L. Nutting	1,328	31.34986	109.05122
Cochise	Herb Martyr Dam, Chiricahua Mts.	Summer/66	F.G. Werner	1,807	31.87105	109.23421
Cochise	Hereford	04/20/87	W.L. Nutting	1,278	31.43882	110.09794
Cochise	Huachuca Mts. (SW) at AZ83 crossing of Copper Canyon	08/20/87	W.L. Nutting	1,843	31.36275	110.30012
Cochise	Lower Pinery Canyon, Chiricahua Mts.	04/08/61	F.G. Werner	1,745	31.96734	109.31915
Cochise	Miller Canyon, Huachuca Mts.	06/28/86	W.L. Nutting	1,760	31.41495	110.27657
Cochise	Pinery Canyon, Chiracahua Mts.	04/21/87	W.L. Nutting	2,142	31.93392	109.27173
Cochise	Pinery Canyon, Chiricahua Mts.	08/14/62	F.G. Werner	2,142	31.93392	109.27173
Cochise	Pinery Canyon, Chiricahua Mts.	06/07/83	W.L. Nutting	2,142	31.93392	109.27173
Cochise	Ramsey Canyon, Huachuca Mts.	04/05/61	W.L. Nutting	1,745	31.44598	110.31088
Cochise	Ramsey Canyon, Huachuca Mts.	06/21/74	F.G. Werner	1,745	31.44598	110.31088
Cochise	South Fork Cave Creek, Chiricahua Mts.	04/24/70	R. Hartley	1,621	31.86914	109.18791
Cochise	Southwestern Research Station, Portal	07/03/74	V. Roth	1,626	31.88203	109.20042
Cochise	Sunnyside Canyon, Huachuca Mts.	07/12/37	E.C. Jacot	1,808	31.44232	110.39639
Cochise	Sunnyside, Sunnyside Canyon, Huachuca Mts. (SW)	08/20/87	W.L. Nutting	1,808	31.44232	110.39639
Cochise	Warren	11/07/41	J.D. Gipson	1,519	31.41415	109.87832
Cochise	Willcox	09/03/58	W.L. Nutting	1,270	32.25528	109.83989
Coconino	48.2 km NW of Flagstaff	06/29/59	W.L. Nutting	1,826	35.65296	112.13905
Coconino	6.4 km E of Flagstaff	10/09/58	M. Messer	2,069	35.21897	111.56137
Coconino	11.3 km W of Flagstaff	10/09/58	M. Messer	2,174	35.24062	111.83183
Coconino	12.9 km SE Tusayan	05/08/87	F.G. Werner	2,021	35.97841	112.12412
Coconino	Flagstaff	10/29/32	G.T. Herrington	2,107	35.20141	111.65433
Coconino	Ft. Valley Experimental Forest	07/02/84	S.C. Jones	2,239	35.26808	111.74571
Coconino	Ft. Valley Experimental Forest near Flagstaff	06/30/59	W.L. Nutting	2,239	35.26808	111.74571
Coconino	Hevlon 19.3 km E of Flagstaff	10/01/58	M. Messer	1,792	35.1612	111.27253
Coconino	Near Woods Canyon, Apache Sitgreaves NF	09/18/84	C.A. Olson	2,295	34.3334	110.93796
Coconino	Oak Creek Canyon near Flagstaff	05/02/34	F. Daper	1,654	34.99617	111.73812
Coconino	Oak Creek Canyon near Flagstaff	10/01/58	M. Messer	1,654	34.99617	111.73812
Coconino	Slide Rock Campground, Oak Creek Canyon	10/12/72	J. May	1,901	34.9174	111.74614
Coconino	Trail Canyon between Jacob Lake and House Rock	06/17/65	F.G. Werner	2,156	36.72862	112.13291
Gila	Haigler Creek, 14.5 km N of Young	06/15/65	F.G. Werner	1,717	34.14818	111.054
Gila	Rose Creek Campground, Sierra Ancha Mts.	10/19/69	J.F. Burger	1,678	33.82789	110.97948
Gila	Sierra Ancha Experimental Forest	05/25/63	J. Burger	1,443	33.78779	110.97186
Graham	17.7 km SE of Solomon	07/27/76	D.S. Chandler	1,238	32.75335	109.35622
Graham	Marijilda Canyon, Pinaleno Mts.	04/07/61	F.G. Werner	1,393	32.69638	109.79055
Graham	Noon Creek, Pinaleno Mts.	04/24/76	D.S. Chandler	1,668	32.63749	109.78678
Greenlee	US 666, 27.4 km N of Morenci	04/19/97	W.L. Nutting	1,217	33.16891	109.26905
Maricopa	Ft. McDowell Indian Reservation	04/05/70	R.C.A. Rice	405	33.54083	111.67476
Maricopa	Ft. McDowell Indian Reservation, Hwy 87 @ Verde River	04/18/70	R.C.A. Rice	423	33.58146	111.66979
Mohave	Limekiln Saddle, Virgin Mts.	10/09/76	P. Words	1,935	36.63592	113.75064
Mohave	South Slope Mt. Trumbull	10/10/78	W.L. Nutting	1,978	36.38423	113.13427
Navajo	4.8 km N of Winslow	10/09/58	M. Messer	1,476	35.14115	110.68671
Navajo	9.7 km E of Snowflake	09/20/77	F.G. Werner	1,762	34.55655	109.97232

Appendix. Continued

County	Collection locality	Date	Collector	Elevation (m)	Latitude (°N)	Longitude (°W)
Navajo	9.7 km E of Snowflake	09/29/77	F.G. Werner	1,762	34.55655	109.97232
Navajo	Five Buttes, 40.2 km N of Holbrook	06/14/61	F.G. Werner	1,766	35.28579	110.06161
Navajo	Holbrook, 1.6 km E on US 180	04/18/87	W.L. Nutting	1,566	34.88679	110.13522
Navajo	Show Low, Silver Creek Road, near Rt. 60	08/16/56	W.L. Nutting	1,960	34.24899	110.04605
Navajo	Winslow	07/28/69	J. Baker	1,504	34.99649	110.68729
Pima	Bear Canyon, Mile 12, Santa Catalina Mts.	03/22/61	F.G. Werner	1,795	32.37427	110.69187
Pima	Bear Canyon, Santa Catalina Mts.	05/06/62	W.L. Nutting	1,795	32.37427	110.69187
Pima	BLM: Empire-Cienega Resource Area	10/21/89	W.L. Nutting	1,432	31.70939	110.58997
Pima	Brown's Canyon, Baboquivari Mts.	08/05/56	W.L. Nutting	1,313	31.7762	111.56419
Pima	Florida Canyon, Santa Rita Mts.	03/01/58	W.L. Nutting	1,490	31.75329	110.84344
Pima	Green Spring, on back road to Mt. Lemmon	08/13/78	F.G. Werner	1,624	32.47739	110.7218
Pima	Hwy Mile 22, Santa Catalina Mts.	07/09/57	F.G. Werner	2,384	32.42647	110.73937
Pima	Lower Madera Canyon, Santa Rita Mts.	04/05/61	W.L. Nutting	1,408	31.73626	110.88244
Pima	Madera Canyon, Santa Rita Mts.	02/16/57	G.D. Butler	1,667	31.73626	110.88244
Pima	Santa Catalina Mts.	07/21/69	W.L. Nutting	2,404	32.44652	110.75833
Pima	Santa Catalina Mts.	08/03/84	W.L. Nutting	2,382	32.42933	110.74369
Pima	Tucson	01/26/34	L.P. Wehrle	730	32.22195	110.97436
Pima	Tucson	07/15/38	L.P. Wehrle	730	32.22195	110.97436
Pima	Tucson	08/08/40	J. Powell	730	32.22195	110.97436
Pima	Tucson	01/15/55	G.D. Butler	730	32.22195	110.97436
Pima	Tucson	02/01/55	G.D. Butler	730	32.22195	110.97436
Pima	Tucson	01/03/56	W.L. Nutting	730	32.22195	110.97436
Pima	Tucson	01/18/58	F.G. Werner	730	32.22195	110.97436
Pima	Tucson	01/27/60	W.L. Nutting	730	32.22195	110.97436
Pima	Tucson	01/27/60	F.G. Werner	730	32.22195	110.97436
Pima	Tucson	01/05/61	F.G. Werner	730	32.22195	110.97436
Pima	Tucson	02/14/62	F.G. Werner	730	32.22195	110.97436
Pima	Tucson	03/16/62	H. Manciet	730	32.22195	110.97436
Pima	Tucson	03/16/63	Ingraham	730	32.22195	110.97436
Pima	Tucson	01/10/66	F.G. Werner	730	32.22195	110.97436
Pima	Tucson	01/18/79	F. Harvey	730	32.22195	110.97436
Pima	Tucson	02/09/79	W.L. Nutting	730	32.22195	110.97436
Pima	Tucson	02/11/79	D. Ullman	730	32.22195	110.97436
Pima	Tucson	04/19/83	W.L. Nutting	730	32.22195	110.97436
Pima	Tucson	09/01/87	B.C. Saliba	730	32.22195	110.97436
Pima	Upper Bear Canyon, Santa Catalina Mts.	03/21/76	F.G. Werner	1,815	32.37793	110.68811
Pima	Vic. Manning Camp, S of Spud Rock, Rincon Mts.	06/24/63	F.G. Werner	2,012	32.1817	110.5411
Pinal	Oracle	07/17/73	V. Guss	1,591	32.58291	110.76096
Pinal	Oracle	06/01/77	V. Guss	1,591	32.58291	110.76096
Pinal	Oracle	09/01/77	V. Guss	1,591	32.58291	110.76096
Santa Cruz	1.6 km SE of Patagonia	02/02/60	W.L. Nutting	1,304	31.53096	110.74307
Santa Cruz	3.2 km N of Ruby Road, Chimney Canyon, Atascosa Mts.	03/23/79	W.L. Nutting	1,269	31.47701	111.24408
Santa Cruz	8.0 km E of Nogales	04/04/61	W.L. Nutting	1,206	31.36275	110.90723
Santa Cruz	Bear Valley, southern slope of Tumacacori Mt.	11/20/55	W.L. Nutting	1,280	31.42991	111.17712
Santa Cruz	Calabasas Canyon, W of Nogales	10/17/60	G.D. Butler	1,251	31.38423	111.04542
Santa Cruz	Canelo Hills, AZ 83, S of Canelo	08/28/87	W.L. Nutting	1,604	31.52285	110.50027
Santa Cruz	Lochiel Road, western slope of Huachuca Mts.	07/13/56	R. Willey	1,687	31.37659	110.40548
Santa Cruz	Madera Canyon, Santa Rita Mts.	06/29/76	M. Dubois	1,667	31.71605	110.87437
Santa Cruz	Madera Canyon, Santa Rita Mts.	06/26/78	W.L. Nutting	1,667	31.71605	110.87437
Santa Cruz	Mt. Hopkins, Santa Rita Mts.	07/08/83	W.L. Nutting	2,401	31.68851	110.88084
Santa Cruz	Patagonia	03/29/58	G.D. Butler	1,236	31.54194	110.7555
Santa Cruz	Sycamore Canyon	08/16/61	W.L. Nutting	1,531	31.38964	110.73918
Santa Cruz	Upper Madera Canyon	03/15/61	W.L. Nutting	1,667	31.71605	110.87437
Santa Cruz	Washington Camp-Pass	04/04/61	W.L. Nutting	1,812	31.38694	110.71191
Yavapai	16.1 km E of Seligman	10/10/58	M. Messer	1,760	35.27229	112.7391
Yavapai	Chino Valley	07/11/39	E.S. Turner	1,424	34.75236	112.43302
Yavapai	Prescott	10/01/58	M. Messer	1,865	34.35653	112.39737
Yuma	Yuma	12/15/57	D.M. Tuttle	69	32.55114	114.55766
Yuma	Yuma	03/02/59	D.M. Tuttle	69	32.55114	114.55766